

Competition between two floating-leaved aquatic plants

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ABSTRACT

Water chestnut (*Trapa natans* L.) is a notorious aquatic invasive species invading wetlands and waterways of the northeastern United States. In the Great Lakes watershed, specifically Lake Ontario coastal wetlands, water chestnut grows in areas similar to the native white water lily (*Nymphaea odorata* Aiton). To understand better the competitive interactions these species may have, they were grown in mesocosms in a factorial design to simulate varying levels of invasion. Biomass, percent cover, number of rosettes or leaves, and specific leaf area of both species, and seed production of *T. natans* were measured and analyzed. Relative growth rate (RGR) was also calculated. These data were analyzed using Spitters' reciprocal-yield model to explore inter-specific and intra-specific effects. Regressions of *T. natans* percent cover, *N. odorata* percent cover, number of *T. natans* rosettes, and number of *N. odorata* leaves against planting density were statistically significant. Inter-specific competition from *N. odorata* was 2.27 times more effective than intra-specific competition on *T. natans* percent cover. These analyses indicate that *N. odorata* exerts more competitive pressure on *T. natans* than *T. natans* on *N. odorata* or either species intra-specifically. However, these analyses also indicate that *N. odorata* may facilitate *T. natans* seed production. Understanding competitive interactions between *T. natans* and other species can help inform management decisions.

1. Introduction

With increasing globalization and climate change, invasive organisms have had compounding effects on ecosystem health and functioning. Exotic plants can often become dominant and form monocultures, which alter habitat structure, reduce biodiversity, and affect nutrient cycling and food webs. Since the 1800s, over 180 exotic species have become established throughout the interconnected Great Lakes, located in east-central North America along the border of the United States and Canada (Pagnucco et al., 2015). Close to half of these exotics have been plants (Mills et al., 1993). Water chestnut (*Trapa natans* L.), an annual aquatic invasive plant, has established populations in the easternmost watershed of the Great Lakes, Lake Ontario. This species can severely inhibit ecosystem functioning and can be costly to control. *Trapa natans* was introduced to North America prior to 1859 from Eurasia as an ornamental. It establishes dense beds of floating-leaved plants that compete with, displace, and reduce native aquatic vegetation, thereby lowering biodiversity (Methe et al., 1993; Strayer et al., 2003). The dense beds that water chestnut creates shade and crowd out native vegetation. The reduction of sunlight available to submersed aquatic vegetation affects the survival of previously

established vegetation and decreases the amount of oxygen released into the water column via photosynthesis (Caraco and Cole, 2002). Water chestnut crowds out useful food sources for wildlife, which results in reduced food quality and availability (Methe et al., 1993; Marsden and Hauser, 2009). The potential change of habitat structure formed by submersed vegetation and reduction in dissolved oxygen affect the densities and communities of aquatic macroinvertebrates. The resulting invertebrate community and water conditions affect the diversity and abundances of fish that can spawn and feed in the vegetation (Caraco and Cole, 2002; Strayer et al., 2003). These habitat changes and adverse environmental effects can be compounded by runoff from surrounding urban and agricultural areas that result in increased nitrogen levels. Net production of water chestnut increases with increased nitrogen levels, which improve the plant's growth and reproduction (Tsuchiya and Iwakuma, 1993).

Water chestnut can cause economic problems in addition to the aforementioned ecological problems. It is estimated to account for an estimated \$200 million in damages and control costs per year in the United States (Pimental, 2005). In Lake Champlain, United States, control measures between 1982 and 2018 involved thousands of volunteer hours and more than \$13 million in state and federal funds

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(Vermont DEC, 2018). In the Potomac River, located in the mid-Atlantic region of the United States, it required more than a half-million dollars over the course of nearly a decade to obtain some measure of control, and although there have been noticeable population reductions, control is on-going (Martin, 1955; Maryland DNR, 2020). Mechanical control has been practiced since the 1960s in Sodus Bay of Lake Ontario and is still currently in use (Mills et al., 1993; Wayne County Soil and Water Conservation District, 2019). These costs do not include economic impacts related to the obstruction of recreational activities and reduction of property and aesthetic values caused by aquatic invasive species.

Water chestnut is considered to be within the eradication or containment categories along the invasion curve in the Great Lakes system (Harvey and Mazzotti, 2014). It is imperative to understand how water chestnut invades systems and competes with native aquatic plants and vital that it is detected and managed rapidly in the Lake Ontario watershed so its spread to the rest of the Great Lakes system, as well as to other water bodies, may be prevented.

In aquatic environments, competition is expected to occur between species with similar growth forms because they occupy similar niches (Gopal and Goel, 1993; Doyle et al., 2003; Zhonghua et al., 2007). In Lake Ontario coastal wetlands, water chestnut grows alongside the native white water lily (*Nymphaea odorata* Aiton), and it is expected that the two species compete for two-dimensional space at the water surface. Water chestnut plants have long, flexible stems and rosettes of floating leaves. White water lily laminae are connected to a rhizome by a long flexible petiole. The floating structures of both species form densely crowded mats of vegetation on the water's surface. These species grow in overlapping water-depth ranges. Water chestnut may grow in water depths from 0.3 m to 3.6 m, although it has been observed to be plentiful in water bodies of 2-m depth (Hummel and Kiviat, 2004). White water lily may also grow to depths of 2 m (Richards et al., 2012). Upon examination in the northeast United States, white water lily beds were found to grow in water depths between 1.9 m and 2.2 m (Sinden-Hempstead and Killingbeck, 1996). Water chestnut is an annual plant and reproduces through seed production. While short-lived annual plants are considered to have *r*-selected traits, water chestnut produces relatively few, large seeds, which is not typical of *r*-selected colonizer species (Kurihara and Ikusima, 1990; Hummel and Kiviat, 2004). However, these seeds are successful, having high germination rates (Phartyal et al., 2018). This reproductive persistence lends itself to being a colonizer or early-successional characteristic (Huston and Smith, 1987). White water lily is perennial and longer-lived than water chestnut. This species may reproduce vegetatively through rhizomes and tubers, as well as via seed production (Wiersema, 1988). These traits are typical of *k*-selected competitors or late-successional species (Huston and Smith, 1987).

As water chestnut continues to grow and spread in the northeastern United States and in the Lake Ontario watershed, it is important to examine how the native white water lily may respond to and interact with water chestnut invasion. In this study, we established mesocosms of monocultures and mixtures of *Trapa natans* and *Nymphaea odorata* at varying densities to determine the presence of and analyze intraspecific and interspecific competition between the two species. We hypothesized that invasive water chestnut would have stronger competitive abilities than white water lily based on growth rate.

2. Methods

A competition experiment was conducted outdoors during the 2014 growing season near the State University of New York–Brockport aquaculture ponds in Brockport, NY. A factorial design was used to grow *Trapa natans* seeds and *Nymphaea odorata* rhizomes, respectively, in the following ratios: 0:2, 0:5, 2:0, 2:2, 2:5, 5:0, 5:2, 5:5 (Fig. 1). There were three replicates of these eight treatments.

The plants were grown in 265-L, round, rubber, stock tubs that contained about 37 l of organic soil, which was collected from the edge

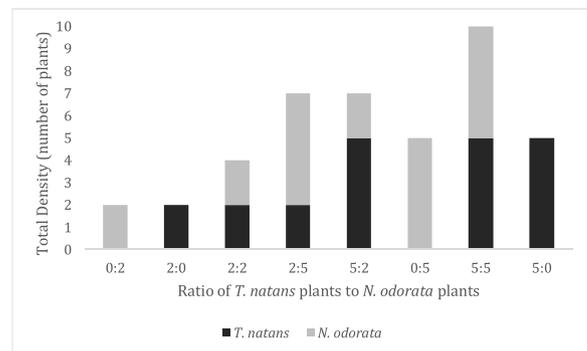


Fig. 1. Factorial design of the competition experiment set-up with varied species densities. Treatments included three replicates of the following combinations of *T. natans* and *N. odorata* plants, respectively: 0-2, 0-5, 2-0, 5-0, 2-2, 2-5, 5-2, and 5-5.

of a marsh near Braddock Bay, Rochester, NY on 10 May 2014. The tubs were filled with pond water from the aquaculture ponds on the same day. *Nymphaea odorata* rhizomes were obtained from Southern Tier Consulting, Inc. on 2 May 2014 and stored in a cool, dark room (about 13 °C) until planted. Evidence of growth was present on all rhizomes, so they were considered viable. *Trapa natans* seeds were collected manually from Braddock Bay, Rochester, NY on 14 April 2014 and stored in a refrigerator at 5 °C until planted. Seeds were tested for viability by visual examination and submerging in water. Floating seeds were not considered to be viable and were not used in the experiment.

The experiment began on 20 May 2014. Each seed and rhizome was weighed to the nearest 0.01 g and placed in the stock tubs. When planted, *Nymphaea odorata* rhizomes were placed just deep enough in the sediment to be covered. Rhizomes ranged between 67.07 g and 210.23 g, and averaged 112.69 g. *Trapa natans* seeds were placed on top of the sediment, as this is where they were found in the field at the time of collection. Seeds ranged between 4.00 g and 5.82 g, averaging 5.00 g. The absolute densities of these 0.65-m² containers were 3 plants/m², 6 plants/m², 8 plants/m², 11 plants/m², or 15 plants/m². Observations on phenology and plant measurements, including height in the water column and percent coverage, were taken throughout the growing season: 27 May, 30 May, 3 June, 5 June, 7 June, 10 June, 12 June, 17 June, 19 June, 21 June, 24 June, 27 June, 3 July, 11 July, 19 July, 25 July, 5 August, 15 August, 19 August, and 28 August. During this time, daylight duration ranged between 13.18 h and 15.10 h. Air temperatures ranged between 8.89 °C and 32.22 °C, and averaged 19.44 °C. Once plants reached the water surface, percent coverage was visually estimated to the nearest 10 % over the surface of the stock tubs for each species. Occurrence of flowering was noted. The experiment was terminated on 1 September 2014.

Entire plants were harvested from the experiment, including roots and rhizomes. *Trapa natans* rosettes and *N. odorata* laminae were considered comparable units upon completion of the experiment, as they formed the floating structures of the plants. Submersed, plume-like structures were present along *T. natans* stems. These lateral structures can be either submerged leaves or adventitious roots and were not included in analyses except when included in biomass calculations. *Trapa natans* rosettes and *Nymphaea odorata* laminae diameters were measured with a ruler to the nearest 0.05 inch (0.13 cm), then the plants, including roots and rhizomes, were placed in plastic zip-lock bags and stored in a refrigerator until they could be processed. Two *T. natans* leaves with petioles and two *N. odorata* laminae were taken from each plant and scanned to determine specific leaf area. The removed leaves and laminae and the remainder of the entire plants were placed in a drying oven at 60 °C for at least 48 h, and dry weights were then measured using a digital scale to the nearest 0.005 g. Leaves and laminae used to calculate specific leaf area were dried and weighed

separately from the rest of the plants. *Trapa natans* plants were weighed together due to tangling, and averaged per replicate. Individual *Nymphaea odorata* plants were weighed and averaged per replicate. Immature and mature *T. natans* seeds found on plants and in the sediment were counted during experiment breakdown. Final observations and counts of *N. odorata* seeds were not made.

2.1. Data analyses

The final, dried biomass of both species, percent cover of both species, number of *T. natans* rosettes, number of *N. odorata* leaves, specific leaf area of both species, and number of *T. natans* seeds produced were analyzed for normality using the Shapiro-Wilkes test and frequency histograms. These variables were then analyzed using the Spitters (1983) reciprocal-yield model. This involved multiple linear regressions in the following forms for each of the variables:

$$1/X_t = a_{t0} + a_{tt}d_t + a_{tn}d_n$$

$$1/X_n = a_{n0} + a_{nn}d_n + a_{nt}d_t$$

In these equations, X_t and X_n may represent the following variables: final dried biomass, percent coverage, number of rosettes or laminae, specific leaf area (SLA), and number of seeds produced. The subscript t refers to *Trapa natans* and the subscript n refers to *Nymphaea odorata*. The respective planting densities for *T. natans* and *N. odorata* are represented by d_t and d_n . The intercepts of the equations, a_{t0} and a_{n0} , represent the inverse of the maximum value of each variable of an isolated plant. The coefficients a_{tt} and a_{nn} represent estimates of intraspecific competition, a_{tn} represents the estimate of interspecific competition as *N. odorata* affects *T. natans*, and a_{nt} represents the estimate of interspecific competition as *T. natans* affects *N. odorata*. A ratio of these regression coefficients (a_{tn}/a_{tt} , a_{nt}/a_{nn}) was determined to show which form of competition was greater by dividing the interspecific competition coefficient by the intraspecific competition coefficient. A resulting number >1 would indicate greater importance of interspecific competition. A resulting number <1 would indicate greater importance of intraspecific competition.

The relative growth rate (RGR) of both species was calculated using the formula:

$$RGR = \frac{(\ln X_2 - \ln X_1)}{t_2 - t_1}$$

where X_2 and X_1 are the percent cover at t_2 and t_1 in days. Percent cover was used instead of dried weight due to the lack of plants available for drying and weighing at the beginning of the experiment. The percent cover was graphed for each species and density treatment over the course of the experiment. Percent cover of both species steadied by day 60, so day 60 was used for t_2 . Day 21 was used for t_1 of *T. natans* and day 14 was used for t_1 of *N. odorata*, which is when each of the species had reached the water surface. A univariate analysis of variance (ANOVA) in a General Linear Model was performed in IBM SPSS Statistics for Windows to determine whether there was a significant difference in the relative growth rate of each species between different treatments.

3. Results

3.1. Plant growth

The experiment took place over 104 days. Daylength ranged between 13 h, 11 min and 15 h, 6 min. Some *Nymphaea odorata* plants reached the water surface within 10 days of planting at the end of May. *Trapa natans* plants reached the water surface in various tubs around 10 June, 21 days after planting. All *T. natans* seeds planted in the experiment germinated. Near the end of June, it became very difficult to distinguish between the individual *T. natans* plants. *Nymphaea odorata* blooms were

first observed on 24 June, 35 days after planting. *Trapa natans* blooms were first observed on 3 July, 44 days into the experiment. Some *N. odorata* laminae began to grow in an aerial form at the beginning of July. Some *T. natans* rosettes also grew in an aerial form in mid-July. Seed development of *T. natans* was observed in mid-July as well, about 60 days after planting. *Trapa natans* rosettes became fragile near the end of August, which aided in the decision to terminate the experiment. *Trapa natans* seed production varied from 3 to 18 seeds per plant, averaging 11 seeds per plant across treatments.

The final wet weight of *T. natans*, averaged per tub due to tangling of plants, ranged between 73.78 g and 447.48 g, and averaged 197.26 g across treatments. The average final dry weight of *T. natans* plants ranged between 11.38 g and 118.96 g per plant and averaged 40.30 g per plant across treatments. Overall percent cover ranged between 10 % and 85 % (or 4%–17% per plant), averaging 30 % (or 9% per plant) cover across treatments. Rosettes ranged from two to eight per plant, averaging four rosettes per plant across treatments. The specific leaf area (SLA) ranged from 97.66–140.19 cm/g and averaged 116.84 cm/g.

The final wet weight of *N. odorata* plants ranged between 292.33 g and 1,484.22 g and averaged 743.70 g across treatments. The final dry weight of *N. odorata* plants ranged between 19.81 g and 875.67 g and averaged 222.18 g across treatments. Overall percent cover ranged between 20 % and 80 % (or 4%–25% per plant), averaging 42 % (or 14 % per plant) cover across treatments. Laminae ranged between five and 13 per plant, averaging nine per plant across treatments. The SLA ranged from 142.07–204.90 cm/g and averaged 173.49 cm/g.

3.2. Competitive abilities

Regression analysis of *T. natans* percent cover, *N. odorata* percent cover, number of rosettes, and number of laminae against planting density had relatively good fits ($R^2 = 0.715, 0.508, 0.628, 0.801$, respectively) and were statistically significant ($p = 0.000, 0.005, 0.001, 0.000$, respectively). The resulting ratios of coefficients of these regressions indicate that, with respect to *T. natans* cover and number of rosettes, inter-specific competition was more important than intra-specific competition (ratio greater than 1). With respect to *N. odorata* cover and number of laminae, intra-specific competition was more important (ratio less than 1). The regressions modeling *T. natans* biomass, *N. odorata* biomass, and *T. natans* seed production against planting density, while mostly statistically significant ($p = 0.041, 0.061, 0.032$, respectively), did not show strong relations ($R^2 = 0.346, 0.311, 0.369$, respectively), although they may still be biologically relevant. The biomass ratios of coefficients similarly show that intra-specific competition was more important with respect to *T. natans*, while intra-specific competition was more important with respect to *N. odorata*. The absolute value of the ratio of coefficients for *T. natans* seeds is also greater than 1, indicating that inter-specific competition was more important than intra-specific competition for this variable. Analysis of the regressions showed poor fit to the model for the specific leaf area (SLA) of either species (Table 1). There was no significant difference among any of the calculated relative growth rates (RGR) when growth was considered in terms of percent cover.

4. Discussion

As anticipated, these two floating-leaved macrophytes, *Trapa natans* and *Nymphaea odorata* compete with each other, particularly with respect to the space they occupy at the water surface. Inter-specific competition from *N. odorata* was 2.27 times more effective than intra-specific competition on *T. natans* percent cover, although there was little effect from *T. natans* on *N. odorata* percent cover or number of leaves (Table 1). In the regression equation of *T. natans* biomass against planting density, the ratio of the inter-specific coefficient to the intra-specific coefficient was 2.5, meaning that one *N. odorata* had the effect of 2.5 *T. natans* plants on *T. natans* biomass. The ratio of the inter-

Table 1

Multiple regression analysis of competition between *Trapa natans* and *Nymphaea odorata*, showing biomass, percent cover, numbers of rosettes, leaves, and seeds, and specific leaf area (SLA). Independent variables in this analysis, d_t and d_n , represent the planted densities of *T. natans* and *N. odorata*, respectively.

1/Variable	Intercept	Intra-specific Coefficient	Inter-specific Coefficient	Ratio of coefficients	R ²	F	p-value
<i>T. natans</i> biomass	0.013	0.002	0.005	2.50	0.346	3.964	0.041
<i>N. odorata</i> biomass	0.003	0.001	0.000	0.00	0.311	3.379	0.061
<i>T. natans</i> cover	0.045	0.011	0.025	2.27	0.715	18.783	0.000
<i>N. odorata</i> cover	0.009	0.027	-0.004	-0.15	0.508	7.757	0.005
<i>T. natans</i> rosettes	0.127	0.030	0.037	1.23	0.628	12.679	0.001
<i>N. odorata</i> leaves	0.035	0.025	0.003	0.12	0.801	30.16	0.000
<i>T. natans</i> seeds	0.072	-0.002	0.270	-135	0.369	4.378	0.032
<i>T. natans</i> SLA	0.009	-0.0000236	-0.0000355	1.50	0.009	0.072	0.931
<i>N. odorata</i> SLA	0.006	-0.0000960	-0.0000325	0.34	0.100	0.834	0.454

specific coefficient to the intra-specific coefficient for *N. odorata* biomass resulted in 0, which means that *N. odorata* plants did not exert a competitive effect against other *N. odorata* plants at those densities. The ratio of the inter-specific coefficient to the intra-specific coefficient for *T. natans* seed production was -135, meaning that the competitive effect of one *N. odorata* plant on *T. natans* seed production was equivalent to 135 *T. natans* plants. The negative ratio indicates a facilitative, rather than competitive effect.

These analyses indicate that *N. odorata* exerts more competitive pressure on *T. natans* than *T. natans* on *N. odorata*, or either species intra-specifically, over the densities used in this experiment. *Nymphaea odorata* plants do not seem to impact the cover or biomass of other *N. odorata* plants and are not impacted by *T. natans* plants, but they do appear to affect cover and biomass of *T. natans*. This supports the reasoning that *N. odorata* may be the stronger competitor of the two species. *Nymphaea odorata* may also negatively affect *T. natans* cover and biomass due to allelopathic activity. Bioassays of the leaves and petioles of *N. odorata* have been found to be inhibitory to plant growth (Gopal and Goel, 1993). However, our analyses also indicate that *N. odorata* may facilitate *T. natans* seed production. Once *T. natans* invades the community, growing conditions within *N. odorata* beds may be beneficial to *T. natans* seed production, allowing for exponential population growth of the invader rather than outcompeting the invader. While *T. natans* may not become dominant in an aquatic community during its first growing season, it could prove to be a strong competitor once its population is established. This supports findings that *T. natans* is capable of surpassing many submersed perennial species in dominance (Groth et al., 1996; Hummel and Kiviat, 2004). In a pond in Japan, *T. natans* was second in dominance only to another floating-leaved plant out of nine species, eight of which were perennial (Kunii and Maeda, 1982). In a competition experiment between *Trapa bispinosa* Roxburgh and *Nymphoides peltata* (Gmelan) O. Kuntze, interspecific interference by *N. peltata* was observed to affect *T. bispinosa*. This was attributed to differences in plant morphology and life-history traits between the two species (Zhonghua et al., 2007). Similarly, our experiment found inter-specific interference by *Nymphaea odorata*, which like *Nymphoides peltata* often reproduces vegetatively and by seed, on *Trapa natans*, which reproduces by seed as does *T. bispinosa*. Neither plant species covered the water surface before the other began to grow, so it was concluded that phenology did not greatly affect the success of either species.

Nymphaea odorata is a competitive species that may resist the invasion of or delay population growth of the invasive species *Trapa natans*. However, *T. natans*, whose success may be attributed to seedbanks of large seeds that have high germination rates (Phartyal et al., 2018), may outcompete *N. odorata* over the course of multiple growing seasons. These results could help guide management efforts to focus on early detection activities in habitats proximal to where *N. odorata* beds occur or are likely to occur. Since these species share habitat preferences, detection efforts should focus on nearshore, calm waters with organic substrates and depths of up to 2 m (Sinden-Hempstead and Killingbeck, 1996; Hummel and Kiviat, 2004; Richards et al., 2012). Locations to search for *T. natans* invaders should include areas already inhabited by

populations of *N. odorata*. Due to the growth habit of *N. odorata*, which may form patches of overlapping floating and aerial laminae (Villani and Etnier, 2008), these populations can make detection of *T. natans* more difficult by visually hiding the floating rosettes of *T. natans*. If populations are detected early in their establishment, there is greater chance of eradication, and effective management will require fewer resources of funding, time, and effort to manage.

Author statement

Kathryn Monacelli: Conceptualization, methodology, formal analysis, investigation, resources, writing- original draft **Douglas Wilcox:** Writing- review & editing, supervision, project administration, funding acquisition.

Declaration of Competing Interest

The authors report no declarations of interest.

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